Evolution in methods of pollination.

ALICE CARTER.

In attempting to arrange our phanerogams in a natural order, I have been astonished at the close resemblance even in external appearance between the reproductive organs of Coniferæ and Pteridophyta; at the Equisetum-like arrangement of the spore cases (anthers and ovules) in many of our exogenous trees, such as Alnus and Betula, whose inflorescences are not highly specialized; and at the return to the moss-like or frond-like form of degenerate water plants, e. g., Lemna, Wolffia and Myriophyllum. The essential similarity in the life processes of all the higher plants, pteridophytes and phanerogams, is a fact familiar since the days of Hofmeister, and is constantly receiving confirmation. For instance, Stengel has recently described the beautiful transition in anatomical structure and origin between the macrosporangia (ovules) of gymnosperms and angiosperms. The discovery of such analogies is one of the great achievements of modern botany, making it possible, by embryology and histology, to trace the ascent from mosses to exogens, picturing to us the development which geology shows has been going on in time.

Variation is the source and presupposition of this development. Change of conditions and cross-fertilization are the two great known causes of variation. The first, in the case of fixed plants works slowly; the second includes within itself the advantages of the first and others of its own; for by it the characteristics of dissimilar parents, whose differences are to a certain extent the results of the dissimilarity of the conditions to which they have been subject, are transmitted in varying proportions to succeeding generations. New properties are thus acquired and old ones changed, and the variable descendants of crossed plants conquer the unimproved offspring of self-fertilization.

The process of conjugation in the lowest plants in which there is a sexual reproduction, in almost all cases makes probable the union of the spores of two distinct individuals (Spirogyra, Mucor, Desmidiaceæ, Diatomaceæ, etc.), while the same possibility of cross-fertilization is insured among the higher thallophytes, liverworts and pteridophytes by motile antherozoids, which are so small that the moisture of the damp places in which the prothallium or sexual generation always grows is sufficient to carry them, sometimes at least, to the germ cells of distinct plants. The wind, too, helps as the means of scattering the asexual spores from which the sexual generation grows.

Among phanerogams the power of elongation of the antherozoid-bearing pollen tube takes the place of the movement of the antherozoid itself, but still the asexual spores of pines, grasses, sedges, and of many forest trees are carried by the wind to the oospheres which they fertilize. Most of these anemophilous plants are probably old types; the Coniferæ, for example, which are all anemophilous, are acknowledged to have been the precursors of the higher monocotyledonous vegetation. They are all anemophilous. Geologists tell us that monocotyledons appeared before exogens; their structure is simpler and they are in many respects a connecting link between these and gymnosperms. Five of the 22 orders of endogens described in Gray's Manual (revised edition) are anemophilous, a large proportion; one is partly wind-, partly water-fertilized; several others are largely hydrophilous, also a primitive method common among degraded water plants such as Vallisneria and many Naiadaceæ.

The very fact that whole orders of endogens have this characteristic of wind-fertilization proves it to be an ancient one, for the features which are common to all members of an order are necessarily as old as the order itself, and the possession of the same property by several orders of a class indicates still greater age. The wide distribution of some of their genera (there is none wider among phanerogams) and the comparative lack in variety of the Cyperaceæ, Gramineæ, Juncaceæ, Eriocauleæ and Typhaceæ point to the one conclusion, that these wind-fertilized endogens are among the oldest of flowering plants.

For somewhat similar reasons many of the anemophilous dicotyls may be considered old types.' They are almost all apetalous—a sign of low development; a sign, too, of old age, for the apetalous was the dominant type of dicotyls in the mid-Cretaceous, forming forty-five per cent of them as against fourteen per cent now. This decrease in numbers is suggestive of extinction and another mark of old age. Further, of the twenty-three apetalous orders represented in our flora, six are anemophilous. These are the Salicaceæ, Cupuliferæ, Myricaceæ, Juglandaceæ, Platanaceæ and Piperaceæ. (Exception must be made of the genus Salix which has developed means of insect attraction). Of these the Salicaceæ are known to be old, for the oldest fossil dicotyledons are of the genera Salix and Populus. None of them include many genera, and this again is a common attribute of old orders and a sign of approaching extinction, according to Darwin's rule that the dominant orders are those of numerous genera and species.

Piperaceæ	include	8	genera	and	1000	species.
Platanaceæ	"	1	"	"	6	"
Juglandaceæ	"	5	"	"	30	"
Myricaceæ	"	1	"	"	35	"
Cupuliferæ	"	10	"	"	400	"
Salicaceæ	"	2	"	"	200	"

The genera are conspicuously few. The Piperaceæ alone have a large number of species and of their method of fertilization I am not sure. The group Saurureæ, represented in our flora, is apparently adapted to wind-fertilization. Moreover many members of the Chenopodiaceæ, Amarantaceæ, Polygonaceæ, Urticaceæ and some Empetraceæ are anemophilous. All this is in marked contrast to the state of things among the younger and more highly developed exogens. For of the 50 polypetalous orders one is partly wind, partly water-fertilized; of the 33 gamopetalous orders, only one is largely anemophilous, and of that one, the Plantagineæ, the typical genus is considered by some authorities to be degraded.

Here, too, the question of color comes to our aid. In every one of these ten apetalous orders the predominance of greenish inflorescences is very noteworthy as a further sign of low organization and of relationship with glumaceous endogens, pines, and pteridophytes. F. F. Mott[1] says that dull color means the absorption of vibrations of every wave length; deep red, deep violet or green that about two-thirds of the wave lengths are absorbed, about one-third reflected; scarlet, yellow, blue or purple that about one-third of the wave lengths are absorbed, about two-thirds reflected. He adds that these three stages of color show therefore three stages of progress in the direction from generalization to specialization, a progress such as marks all development. Accordingly we should expect to find, as we do, greenish and dull shades prevalent among the least highly organized, and

[1] American Naturalist, Sept. 4, 1890.

therefore, other things being equal, the oldest inflorescences. On the other hand, among the dominant forms of to-day, the greatly specialized Compositæ, Umbelliferæ, Leguminosæ, Orchidaceæ, Labiatæ, Scrophulariaceæ, Rubiaceæ, Ericaceæ, etc., bright reds, blues and orange yellows are common. There are 23 orders of the world flora which contain 1000 species or more. Inconspicuous flower clusters are characteristic of only five of these, viz: the Cyperaceæ, Gramineæ, Urticaceæ, Piperaceæ and Euphorbiaceæ. The first and second are very old types, the third and fourth apetalous (probably old), the last degenerate.[1] It seems then logical to call these inconspicuous, little protected clusters of stamens and pistils ancient forms of flowers and to consider wind-fertilization, which is so common among them, a primitive method.

But the crossing of individuals must be a most desirable thing if it is to be obtained at such enormous cost, for pollen is precious material, yet for every grain which the wind carries to an ovule thousands are swept to destruction. Self-fertilization would apparently be a much surer and cheaper process. The end, however, justifies the means, otherwise crossed plants would long ago have yielded place to self-fertilized victors. Darwin, by a most careful and elaborate series of investigations of more than a thousand plants, has shown that "wherever plants which are the offspring of self-fertilization are opposed in the struggle for existence to the offspring of cross-fertilization, the latter have the advantage. In no single case was the advantage on the other side."[2] So wind-fertilized plants waxed strong and multiplied on the face of the earth.

Meanwhile "away back in the darkness of the coal period, when tree-ferns, calamites and giant club-mosses combined with archetypal yews to people the steaming swamps of a hot, cloud-laden island world, there existed a strange form of insect which can only be compared to the cockroaches of our day, but which seems to have embodied in its structure the beginnings of all the varied types of insect life, the promise and

[1] White and yellow are the predominant colors of our own flora; 420 yellow, 614 white species among the 2056 flowers of Gray's Manual (revised edition). It would be interesting to know whether there is a larger proportion of reds and blues in the tropical lands where flower-frequenting birds and butterflies are more abundant. Wallace's statement of the surprising monotony of tropical vegetation is not necessarily opposed to this.

[2] H. Müller.

prophecy not only of our dragon-flies, and beetles, but also of our flies, bees and butterflies."[3] Scudder sums up what was known of American fossil insects about nine years ago in this way: "The species of fossil insects known from North America number eighty-one; six of these belong to the Devonian, nine to the Carboniferous, one to the Triassic and sixty-five to the Tertiary epochs; the Hymenoptera, Homeoptera and Diptera occur only in the Tertiaries; the same is true of the Lepidoptera, if we exclude the Morris specimen, and of the Coleoptera with the Triassic exception. The Orthoptera and Myriopoda are restricted to the Carboniferous, while the Neuroptera occur both in the Devonian and Carboniferous formations." Packard says: "the lower forms of Hymenopera, so far as the scanty records show, appeared first in the Jura formation."

From these statements its seems probable that the period of the appearance of dicotyledons was also the time of the development of our great groups of insects. The two have been hand in glove ever since. Insects wandered to and fro seeking what they might devour, and if the man is blessed who makes two blades of grass grow where only one was, thrice happy is the insect which discovers an entirely new source of nourishment by which its food supply is many times multiplied. Accidentally lighting on a staminate flower cluster, as I have seen bees and flies do on the wind-fertilized inflorescences of Poterium Canadense, it finds itself in the land of plenty and thereafter is on the outlook for food-magazines of the same kind. The flowers with highly colored bracts (represented in the flora of to-day by some species of Euphorbia and Amarantus), or those with colored stamens, (such as species of Thalictrum, Corema and Plantago now show as the first step toward insect attraction), being more conspicuous will be more frequently visited. Visitors leaving the flowers carry with them pollen which clings to the hairs of their bodies, and some of this will occasionally be left on the feathery stigmas of the pistillate clusters which will also be visited, at first in vain. The ovules so fertilized ripen seeds which inherit the peculiarities of their parents to a greater or less degree.

This is then, as far as we know it, the story of the origin of flowers, which were at first merely axes bearing spirally ar-

[3]Lester F. Ward.

ranged reproductive organs, such as the antheridial and archegonial clusters of mosses or the spore-bearing stalks of ferns and equisetums. The growth of bracts, i. e., leaves altered to do protective work, and the further development in the macrosporangium mouth of the mucilaginous secretion already foreshadowed in the archegonia of ferns, produced the characteristic inflorescences of gymnosperms. The position of a plant, as of a man, in the scale of progress, is measurable by the protection given to the children and by the manner of their preparation for independent life. The increase of ovule-shelter by the formation of a closed ovary is an easy step, as the comparison of the ripened pods of Mitella, Tiarella, Aquilegia or almost any of the Leguminosæ with the ovule-bearing scales of pines, shows. By the incurving of the edges of one of these scales, or more probably, by the persistence of the inrolling of the edges of the young leaf, an ovary perfect in every essential would be produced, and the favorable variation transmitted to succeeding gererations.[1] Still further provision for the safety of the seeds and for their advancement in life, is attained by increased development of the protective bracts to form organs such as the perigynia of sedges, the glumes and awns of grasses, the hairs of Eriophorum, etc.; more complete adaptation to wind-fertilization by the formation of microsporangium stalks (filaments, sometimes feebly developed in the Coniferæ) and of feathery outgrowths (stigma) from the united tips of the carpellary leaves.

Then the lords of horticulture, the insects, with an eye to profit, began their investigations of the fields, at first obtaining only pollen from these wind-tossed inflorescences. In some cases they never find anything more, e. g., in Hepatica and Papaver. But the occurrence of sugary secretions,

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[1] Some time after writing this sentence, I came across a remarkable confirmation of the truth of the theory in Eichler's "Blüthendiagramme," part II, p. 216. He says: "In most Resedaceae the carpels are so united that they form a one-celled ovary with parietal placentae, . . yet they remain free from one another at the top, nor do the edges of the individual carpels close together there, so that the ovary is open above. . . . The condition of things is somewhat different in Reseda luteola, Caylusea and Astrocarpus. In the first species the individual carpels remain separate, their edges turned inwards and meeting below to bear the ovules in the ordinary way, but not touching above so that each carpel is open far down on its inner suture. In Caylusea there is neither union of the carpels, nor closing together of the edges of each one separately; the ovary *appears therefore to be made of five or six free scales which stand in a circle*—a very primitive structure, not occurring elsewhere in this form." The state of things in Tiarella cordifolia seems to me to correspond well to this description of the pistils of Reseda luteola.

common elsewhere, as on the petioles of the passion vine and on the leaves of the larch where bees busily search for them, among the floral organs is a not surprising result of the energy of the currents which nourish anthers and ovules.[1] Such secretions at first perhaps not abundant, nor perceptibly sweet, will be gradually increased and improved by means of this co-working of plant and insect. Stages in the evolution of nectar and of nectar-protecting organs are represented to-day, steps which connect the watery fluid found exposed the first day of blossoming in the stigmatic cavity of Nymphæa tuberosa, the drops of liquid at the bases of the carpels of Caltha, the honey protected by scales on the petal bases of Ranunculus and by elongated petal-bases (i. e. spurs) of Aquilegia, etc., with the showy buckets of Marcgravia from which the brilliant sun birds of India drink nectar worthy of the gods.

The result of this long-standing partnership is, that, in the place of a world of green, corolla-less flowers, our meadows are rich with the gold of daisies and buttercups; our hillsides, covered with the blue of innocence; our rocks, purple with clematis, or gay with columbine; asters and golden-rods reflect royal colors in the brooks; gentians give back the blue of the sky from the mountain pastures; and there are glorious fringed orchids for those who can find them, and they are the bees and butterflies. For the good poet was mistaken in supposing that many a flower is born to blush unseen. The bees who have made it blush will surely be there to see.

Ithaca, N. Y. [*Concluded next month.*]

Mt. Kataadn and its flora.

F. LAMSON-SCRIBNER.

In August, 1874, a party of gentlemen from Bangor and Orono, under the direction of President M. C. Fernald of the Maine State College, made the ascent of Mt. Kataadn for the purpose of determining more accurately than had before been done, the altitude of the mountain. This work was accomplished by Prof. Fernald in a very thorough and accurate manner, and his observations were made public at that time.

Mr. F. W. Hardy, a well known photographer of Bangor,

[1] cf. BONNIER: Comptes Rendus, LXXXVIII. 662.